

A MIDDLE JURASSIC MAMMAL BED FROM OXFORDSHIRE

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ABSTRACT. The geology, palaeoecology, and vertebrate fauna of a mammaliferous sediment in the Forest Marble of Oxfordshire are described, as are the techniques used in its processing. The mammalian fossils appear to have been derived from the faeces of predatory animals, probably small theropods, the occurrence of theropod teeth possibly having value in the search for new Mesozoic mammal localities. In the mammal (s.l.) fauna from the new site there occur late representatives of the Morganucodontidae (*Wareolestes rex* gen. et sp. nov.), Kuehneotheriidae (*Cyrtatherium canei* gen. et sp. nov.), and Tritylodontidae, as well as the earliest known members of the families Dryolestidae and (?)Peramuridae (*Palaeoxonodon ooliticus* Freeman, 1976). The holotype of the (?)peramurid appears to show an early stage in the development of the talonid basin. The first known upper molars of Middle Jurassic representatives of the suborders Amphitheria and Docodonta are described and illustrated, as are the positions of the wear facets thereon. The mammals now appear to have diversified at the level of the family long before the Bathonian, and probably during the early Jurassic.

IN recent years there has been a revival of interest in the mammalian faunas of the Mesozoic formations, an area of study largely dormant since the publication of the classic monographs of Owen and Simpson in 1871 and 1928/9 respectively. The recent large increase in both the quantity of fossil material and in the number of productive localities has been due principally to the introduction of various techniques for the processing of sediments on a large scale.

In spite of this increased level of activity, the known mammalian fauna of the Middle Jurassic has not been substantially increased since the nineteenth century, when the first Mesozoic mammals known to science were found by the miners working the Stonesfield Slate. The only major addition published since then has been the fauna from the Great Estuarine Series of Skye, (Waldman and Savage 1972).

Nevertheless the British Middle Jurassic seems to abound in fossil mammalia and I have managed to add another three mammaliferous localities to the two previously known, one in Dorset (Freeman 1976*a*) and two in Oxfordshire (Freeman 1976*b*). Undoubtedly, many more such localities must await discovery.

The following account deals with the most significant of the three sites, the one in the Forest Marble of the Old Cement Works Quarry, Kirtlington, Oxfordshire (SP 494200).

STRATIGRAPHY

The Kirtlington Old Cement Works Quarry has been disused since 1929 (Dodsworth 1972), but still provides a highly fossiliferous exposure of the White Limestone, Forest Marble, and Cornbrash. Together with similar quarries in the neighbourhood, it has been the subject of numerous papers on Middle Jurassic geology and palaeontology. Notable among these are the works of Arkell (1931) and McKerrow, Johnson, and Jakobson (1969). The better exposure available to Arkell permitted a section to

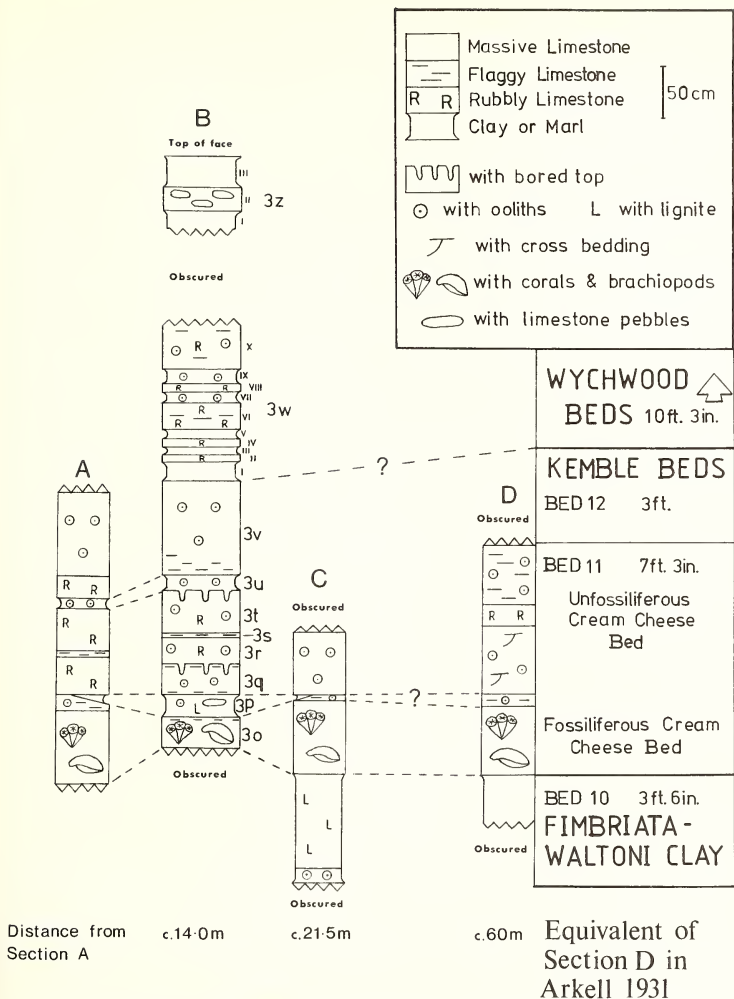
be measured which facilitated correlation with other exposures in Oxfordshire and Gloucestershire. Since then, the main face of the quarry (the east face) has deteriorated to the point where the more detailed stratigraphical and palaeoecological study of McKerrow *et al.* (1969) had to be confined to scattered exposures away from Arkell's area of study. The following remarks are primarily concerned with establishing the stratigraphic position of the mammal bed, in both the immediate context of the quarry, and more generally in the regional context; they do not extend to such problems as the position of the White Limestone/Forest Marble junction, nor the subdivision and long-range correlation of the Forest Marble (see Odling 1913; Richardson, Arkell, and Dines 1946; and Palmer 1973).

The bed of unconsolidated brown marl which has yielded the mammalian fossils is without doubt that labelled 3p in McKerrow *et al.* (1969); in the present account it is named the Kirtlington Mammal Bed. It is impersistent in its occurrence, forming a lenticle in the north-eastern corner of the quarry with a total outcrop of 21.5 metres (see Pl. 15, fig. 1). The bed is of variable thickness (c. 4 to 25 cm); at its extremities it rapidly thins away to nothing, being replaced from below by an increasingly greater thickness of a deep-yellow friable oolitic limestone which here, and elsewhere along the outcrop, grades downwards into the massive 'Coral Epithyris Limestone' (3o) of McKerrow *et al.* (1969). A similar friable yellow limestone occurs immediately above the mammal bed. The contact of the mammal bed with the soft limestones above and below it are extremely abrupt, which suggests that the contacts are erosional features.

From its position overlying the 'Coral Epithyris Limestone' (=Arkell's 'Fossiliferous Cream Cheese Bed'), the Kirtlington Mammal Bed would seem almost certainly to be laterally equivalent to part of the 'Kemble Beds' shown in Arkell's 1931 section. More specifically, as can be seen from text-fig. 1, it seems likely that it is at the same stratigraphic level as a thin bed of friable oolitic limestone sandwiched between the 'Fossiliferous' and 'Unfossiliferous Cream Cheese' beds at the northern end (i.e. left-hand side) of Arkell's 1931 section (q.v.).

In the broader context, as the ascending sequence of the Great Oolite Group in the Oxford area is Chipping Norton Formation-Sharp's Hill Formation (including the Stonesfield Slate)-Taynton Limestone Formation-Hampden (Marly) Formation-White Limestone-Forest Marble-Cornbrash (McKerrow and Kennedy 1973), the new mammal fauna is clearly slightly younger than that from Stonesfield. As ammonites have not been reported from the Forest Marble of the Kirtlington area, the mammal bed cannot be ascribed to any of the Bathonian ammonite zones directly. However, using indirect evidence, the occurrence of the ostracod *Glyptocythere penni* in the fimbriatus-waltoni Clay at Kirtlington (see text-fig. 1) has led Bate and Mayes (1977) to suggest that this formation belongs in the *Clydoniceras discus* Zone. If so, as the Lower Cornbrash contains this zonal ammonite, the beds between the fimbriatus-waltoni Clay and the Lower Cornbrash, among them the Kirtlington Mammal Bed, must also be assigned to the *C. discus* Zone. The contrary opinion of Torrens (1969) places the Kemble Beds (and therefore presumably the mammal bed) in the underlying *Oxycerites aspidoides* Zone (Upper Bathonian).

Further afield, the age relationships of the Kirtlington mammals to those described elsewhere from the Middle Jurassic are at present known only approximately. As



TEXT-FIG. 1. The short-range stratigraphy of the Kirtlington Mammal Bed. Section B corresponds in part to the upper part of Profile 3 of McKerrow *et al.* 1969, as does the numbering of beds 3o to 3v. The mammal bed is bed 3p. Sections A and C show the north-west and south-east extremities of the bed, while Section D corresponds to part of the northern extremity of the section in Arkell 1931.

Waldman and Savage (1972) consider that their mammal site in the Isle of Skye is of Middle Bathonian age, it would appear to be slightly older than Kirtlington, which presumably is roughly contemporary with the other known Forest Marble site, at Watton Cliff in Dorset (Freeman 1976a).

SEDIMENT PROCESSING

Individual batches of the mammal bed were slurried with water, either by boiling for a short time or by soaking in cold water overnight, and were then sieved through a 0.35 mm mesh. After cleaning the shelly residues by washing with aqueous detergent solutions, they were dried and resieved into narrow size-range fractions of which the coarser (>2.1 mm) were hand sorted without further treatment. The remaining fractions down to 0.5 mm were digested with aqueous acetic acid (15% by volume), to leave residues consisting almost entirely of particles of limonite and vertebrate fossils.

These residues were so concentrated (0.10% of the original sediment weight) that further concentration was not necessary, the vertebrate fossils being easily isolated by simple naked-eye searching under natural daylight.

However, purely as an experiment, two different techniques were applied to separate batches of one of these acetic acid-insoluble residues in order to remove the limonite, and thus concentrate the vertebrate fossils still further. The first batch was density separated using bromoform (density $2.63\text{--}2.69\text{ g ml}^{-1}$ at 20°C). The floating fraction constituted 51% by weight of the original and still consisted of a mixture of limonite and fossil bone, albeit enriched in the latter. Moreover, the movement of the bone into the floating fraction was not complete, some remaining in the fraction denser than bromoform. The second batch of acetic acid-insoluble residue was treated with an aqueous solution of thioglycolic acid (5% by volume), which had been pre-treated with powdered modern bone (see Rixon 1976, p. 112). The limonite dissolved almost totally, the undissolved bony residue constituting 19% by weight of the original. Thus treatment with thioglycolic acid was considerably more effective (enrichment factor 5.3) than was the bromoform flotation (enrichment factor 2.0) in the further enrichment of the vertebrate-containing residue.

INVERTEBRATE PALAEOLOGY, LITHOLOGY, AND PALAEOENVIRONMENT

The Kirtlington Mammal Bed appears to contain assemblages of both indigenous and derived fossils. The latter, characterized by their abraded condition and the frequent presence of patches of adhering oolitic limestone matrix, comprise fragments of oysters and such typically marine forms as compound corals, polyzoa, brachiopods, echinoids, and crinoids. It is evident that these derived fossils originated from one or more of the marine limestones lower in the Great Oolite sequence, very probably the White Limestone.

In contrast, the indigenous biota appears to be of non-marine origin. Apart from the bulk of the vertebrate fauna (q.v.), the indigenous fossils are largely microscopic, comprising abundant charophyte gyrogonites and ostracods. This ostracod

fauna has been examined in detail by Dr. Martin Ware (Ware 1978), who reports that it contains, amongst others, the species *Timiriasevia mackerrowi* (abundant) and *Theriosynoecum kirtlingtonense*, both of which were considered by Bate (1965) to be freshwater forms; as both species show the characteristic population age structure expected of autochthonous species, they provide good evidence for the freshwater origin of the mammal bed.

Small indeterminate plant fragments occur abundantly as sooty or limonitic impressions in the mammal bed. A casual search for more complete plant remains, and for insect fossils, has so far been unsuccessful.

The mammal bed contains an apparently unsorted mixture of clastic materials, ranging in size from subangular pebbles of oolitic limestones down to abundant comminuted shell debris, individual ooliths, and rare silica sand grains. Particle-size analysis of the sediment shows it to be remarkably uniform in texture, both vertically and horizontally, over the whole outcrop (see Table 1), and thus to be free of large-scale current sorting. Apart from localized and minor concentrations of comminuted shell and ooliths along individual bedding planes, no sedimentary structures have been seen; in particular, there is no sign of cross-bedding.

The mammal bed contains iron in the +3 oxidation state (as limonite), rather than in the +2 oxidation state (as in iron pyrites), suggesting that deposition occurred under oxidizing rather than reducing conditions.

Mr. Noel Shelton of GR-Stein Refractories Ltd. has investigated the mineralogy of the <0.35 mm fraction of the sediment by X-ray diffraction (X.R.D.). He reports that it consists largely of calcite, with a subordinate amount of quartz, findings which were supported by both the loss-on-ignition results (34.23%), and qualitatively, by acid digestion. No clay minerals were detected by X.R.D. My own analysis of the <0.35 mm fraction by acid-base titrimetry gave a CaCO₃ content of about 66–68% (by weight). Sugden and McKerrow (1962) discussed the composition of marls within

TABLE 1. Particle-size analysis of the residues from the Kirtlington Mammal Bed, showing its uniformity of texture both horizontally and vertically.

Source of sediment, distance from Section A (metres)	Weight of sediment (kg.)	Mesh analysis of washing residues as percentages of initial sediment weight							
		>0.5in	0.5 – 0.25in	0.25in – 2.1mm	2.1 – 1.7mm	1.7 – 1.4mm	1.4 – 1.0mm	1.0 – 0.5mm	0.5 – 0.35mm
0 – 0.85	7.4	0.19		0.64	0.28	0.25	0.82	1.22	2.35
c. 4.3	165.7	0.03	0.09	0.42	0.21	0.16	0.58	1.01	2.34
10.4 – 17.2	207.5	0.21	0.21	0.52	0.25	0.19	0.66	1.20	5.60
17.2 – 20.2	401.6	0.15	0.13	0.51	0.23	0.17	0.63	0.97	2.09
c.18, top half of bed	2.819	0.50			0.18	0.12	0.39	0.88	1.71
c.18, bottom half of bed	2.462	0.48			0.18	0.13	0.47	0.98	1.88

the Great Oolite Series of Oxfordshire, concluding that the substantial proportion of clay in such sediments, by forming films around the crystals of calcium carbonate, prevents its recrystallization and thus inhibits the induration of the sediment. The non-detection of clay minerals in the Kirtlington Mammal Bed by X.R.D. is therefore surprising, as the sediment displays all the properties mentioned by Sugden and McKerrow as typical of marls. Thus it is friable when dry, becoming plastic when wetted with water. In other words, in the apparent absence of clay minerals, it is not clear what has prevented the induration of the sediment.

It seems probable that during a temporary marine regression, a shallow, non-stagnant body of freshwater received periodic influxes of poorly sorted sediment which consisted largely of calcite mud, and which was obtained locally by the erosion of earlier Middle Jurassic oolitic limestones.

THE VERTEBRATE FAUNA OF THE MAMMAL BED

In order to prepare a vertebrate faunal list a sample of the mammal bed weighing 141.9 kg was processed by the standard method described earlier, and the residues hand picked as quantitatively as possible down to a particle size of 0.5 mm. The vertebrate fossils were sorted into their respective categories, and both complete and incomplete specimens counted and weighed. In the context of this faunal list (Table 2), and Tables 3 and 4, an 'incomplete' specimen is regarded as one whose missing portion could reasonably be expected to be isolatable and identifiable. Certain items in Table 2 do not appear to be even approximately representative of the sediment as a whole; such unrepresentative occurrences are indicated where appropriate. The remarks following apply to the vertebrate fauna *in toto*, and not just to that in Table 2.

Virtually all of the vertebrate fauna appears to be truly indigenous to the mammal bed, rather than being derived from the oolitic limestone clasts that occur so abundantly in the deposit, a 78.5 g hand-picked sample of these clasts yielding only thirteen minute fish scales by acid-digestion. Similarly, as care was taken whenever possible to remove the soft limestones that tended to adhere to the top and bottom surfaces of the mammal bed, contamination from these sources should also be minimal.

Nearly all of the abundant crocodilian teeth are shed crowns, only three of the 468 complete teeth in the faunal list having roots. This, coupled with the absence of wear other than that produced by use, suggests that the accumulation of the crocodilian teeth was largely a biocoenosis. They vary in shape from sub-conical to elongated and strongly recurved, and range in crown height from 0.8 to 9.5 mm. A pair of carinae usually extends to the apex of each tooth, the enamel of which is ornamented with vertical striae; this ornamentation varies markedly in its degree of prominence, suggesting that more than one species is represented. The teeth bear little resemblance to those of the *Teleosaurus* spp., marine crocodilia which have been found in the Bathonian of Oxfordshire (Phillips 1871), but instead are similar to the teeth of the small Late Jurassic freshwater goniopholid *Nannosuchus*. The status of this latter animal is uncertain, being regarded by its original describer, Owen (1879), as a new genus with adults dwarfed to match the size of the mammals upon which Owen

TABLE 2. Vertebrate fossils from 141.9 kg of the Kirtlington Mammal Bed, by weight and number: ≥ 0.5 mm.

TEETH	Number	Weight	% by wt.	OTHER REMAINS	Number	Weight
MAMMALIA (s.l.)	5 + [4]			REPTILIA		
REPTILIA				Cetiosaurus (?) bone *	[4]	1535g
Crocodylia	468 + [208]	2.6046g	75.17	Crocodylian scutes	[45]	1.4061g
Ornithischia, type A	19 + [10]	0.2251g	6.50	Crocodylian (?) vertebrae	19 + [19]	0.9392g
Ornithischia, type B	4 + [1]	0.0627g	1.81	Crocodylian (?) claws	11 + [3]	0.2113g
Theropoda *	2 + [3]	0.0192g	0.55	Chelonian plates	2 + [89]	10.99g
Pterosauria	8	0.0145g	0.42	Lepidosaurian jaws	[48]	0.0804g
Incertae Sedis	5 + [22]	0.2536g	7.32	AMPHIBIA		
ACTINOPTERYGII				Anuran limb bones *	[3]	0.0350g
Lepidotidae + Pycnodontidae	51 + [8]	0.1953g	5.64	ACTINOPTERYGII		
?Caturus sp. *	6	0.0034g	0.10	Scales	>197 + [>59]	>0.7109g
ELASMOBRANCHII				Vertebrae	6 + [1]	0.0259g
Asteracanthus sp. *	1	0.0824g	2.38	CLASS INCERTAE SEDIS		
Hybodus sp. *	2	0.0042g	0.12	Vertebrae	9	0.0729g
"Lamnid" *	1			Long Bones	19 + [>228]	>0.7117g
TOTAL		3.4650g	100.01	Miscellaneous		>10.0g

Square brackets enclose the numbers of 'incomplete' specimens as defined in the text. An asterisk indicates that the specimens concerned were present in an atypically high concentration in the particular batch of sediment analysed. The fossils identified as Lepidosaurian jaws may also include those of small fish.

considered they preyed, while a later worker, Joffe (1967), suggested that *Nannosuchus* was merely an assemblage of juvenile specimens of *Goniopholis simus*. In an earlier paper (Freeman 1975), I adopted a non-committal attitude towards this problem, but pointed out the seeming paradox of the remains of crocodylia in a Lower Cretaceous lignite bed greatly outweighing those of their likely prey; this imbalance is again to be seen in the fauna of the Kirtlington Mammal Bed. The supposed crocodylian vertebrae are amphicoelous, and are of the right order of size to be from the same animals as the teeth, as are the dermal scutes and claws.

Of the ornithischian teeth, type A closely resembles those of the Early Liassic ?ankylosaur *Scelidosaurus* (Swinton 1973) and the Late Jurassic hypsilophodont *Echinodon* (Owen 1861); they range in crown height from 0.8 to 5.2 mm. Type B are of the same general size and shape as type A, but do not have cutting edges which are crenulated, nor crowns which are vertically ribbed. It is not clear whether these differences are of taxonomic significance or are merely the result of wear upon type A teeth, although the former is suspected.

The theropod teeth, with only one exception, are smaller than those of the Middle Jurassic carnosaur *Megalosaurus bucklandi* ranging in height from 1.6 to 7.4 mm. They may be the teeth of either juvenile *M. bucklandi* or of coelurosaurs. The possible ecological significance of these theropod teeth is discussed later.

Three incomplete long bones are identified as the fused tibia/fibula or radius/ulna of anurans. This skeletal modification is known in the Early Jurassic anuran *Neobatrachus* (see Romer 1966, fig. 145), and so the Kirtlington specimens add nothing to the evolutionary history of the order. Their only significance is to suggest that deposition of the mammal bed took place under non-marine conditions, as does the greater part of the vertebrate fauna in general.

THE ORIGIN OF THE MAMMALIAN FOSSILS—?COPROCOENOSIS

Mellet (1974) noted the similarity in preservation between the contents of recent carnivore 'scat', and terrestrial microvertebrate fossil accumulations, and advanced the hypothesis that the latter were composed predominately of the contents of the faeces or regurgitata of predators. He proposed a term, 'coprocoenosis', to describe such an accumulation. The observations described below support Mellett's ideas and suggest that they may be of value in the search for new Mesozoic mammal sites.

The Kirtlington Mammal Bed was of necessity processed in individual batches, ranging in weight from 36.1 to 141.9 kg, each batch being collected from a relatively small area of accessible outcrop. Unexpectedly, it was found that the similarity between the mammal teeth *within* an individual batch tended to be greater than *between* batches (see Table 3). This phenomenon, only weakly displayed at Kirtlington, has been seen by the author in a more striking form elsewhere. Furthermore, the isolated mammal teeth frequently appear to have been hollowed out from within, their pulp cavities being greatly enlarged. In some cases this process has resulted in the destruction of the roots of the teeth, leaving only the hollowed-out husks of the highly durable, enamel-coated, crowns. Most of the mammal teeth from Kirtlington have incomplete crowns, the fractures being always sharp and fresh looking. The absence of matching fragments of these broken teeth and the generally good condition of the non-mammalian fossils suggest that most of the damage suffered by the mammal teeth was not caused by the isolation procedures, but instead pre-dates fossilization. Finally, one edentulous fragment of a mammalian dentary has been found which bears on its external surface two circular depressed fractures, of approximate diameters 0.9 and 0.4 mm, which appear to be the marks of a predator's teeth.

It therefore seems likely that the mammals of the Kirtlington Mammal Bed were largely the victims of predators. The action of digestive juices in the predator's

stomach would usually destroy all the non-compacted bone in the prey, leaving only the relatively resistant teeth to be excreted. Even these would usually be broken and partially digested. However, the enclosure of the teeth within a faecal pellet would protect them from further damage, and provide them with a buoyant vehicle for water transportation to an environment suitable for their fossilization. Burial and subsequent oxidative decay of the faecal pellet would then liberate the teeth as independent but spatially associated entities.

The similarity of the teeth within a given batch of sediment may therefore be the result of original association within the same faecal pellet, and working backwards, even within the jaws of the same individual animal. This suggests that careful batch-wise processing of mammaliferous sediments might occasionally yield worthwhile evidence of association between various parts of mammalian dentitions.

As to the identity of the predators responsible, I suggest that they were primarily small theropods, either coelurosaurs or juvenile carnosaurs. At Kirtlington, teeth of small theropods are rarer even than those of mammals and occur in the same sporadic way in the sediment (see Table 3), suggesting that the same erratic mechanism (?coprocoenosis) was responsible for the fossilization of both groups of animals.

TABLE 3. Distribution of teeth of mammals, theropods, and ornithischians between individual batches of the Kirtlington Mammal Bed, suggesting a possible coprolitic origin for the mammal teeth.

TAXON	WEIGHT OF BATCH	44.6 kg.	141.9 kg.	39.5 kg.	49.9 kg.	137.3 kg.	76.6 kg.	36.1 kg.
<i>Palaeoxonodon ooliticus</i>			6	9 ⁷ 7 ⁸	12		36	
? <i>Amphitherium</i> sp.					16			
Dryolestidae					14		29	
<i>Cyrtolatherium canei</i>		11	38		27?			
Eupantotheria incert. sed.					26	31?	32	
<i>Wareolestes rex</i>					25			
Morganucodontidae inc. sed.					18	23	60	
Docodontidae	1 ² (2)	5	17	13	24	61		42 ⁴³ 40
Triconodontia incert. sed.		54?			15	19	22	
Tritylodontidae		3	6?	10			34	37
Mammalia (s.l.) incert. sed.		53	52	34	62	43	20	21
MAMMALIA, no. of teeth	[two]	five + [four]	four + [one]	one + [four]	seven + [nine]	three + [six]	[four]	
THEROPODA, no. of teeth	one + [one]	two + [three]	none	two	none	two + [one]	none	
ORNITHISCHIA, no. of teeth	ten + [two]	twenty three + [eleven]	nine + [one]	twelve + [one]	twenty nine + [six]	sixteen + [three]	nine + [two]	

Note the irregular distribution of the mammal and theropod teeth compared with that of the ornithischian teeth. Note also the greater degree of fragmentation of the mammal teeth (square brackets enclose the numbers of 'incomplete' specimens as defined in the text).

Symbols: upright semicircles=lower molars; inverted semicircles=upper molars; diamonds=pre-molars; circles=cheek teeth of uncertain position; rectangles=incisors; triangles=tooth fragments of uncertain position. The numerals enclosed within these symbols are the 'FM/K' numbers of the specimens.

This contrasts with the occurrence of the other important group of terrestrial vertebrates, the ornithischians, whose teeth are present in a high and relatively constant concentration (one tooth per 3.3 to 4.2 kg). Further afield, mammal fossils occur with those of theropods not only at Kirtlington, but also in the Cliff End Bone Bed (author), and in sediments from Swanage (Simpson 1928, p. 190), Watton Cliff, Dorset (personal communication from David Ward), Woodeaton Quarry, Oxfordshire (observations of author and David Ward), Stonesfield (Buckland 1824), and Hanover Point in the Isle of Wight (personal communication from Richard Ford; see Butler and Ford 1977). No other terrestrial groups are consistently associated with one another in this way. With the exception of the Stonesfield *Megalosaurus*, the teeth of the theropods are small and are thus compatible with a diet of small mammals.

Even irrespective of any possible predator/prey relationship, considered empirically, the presence of theropod teeth within a sediment would suggest that mammal fossils are also present. Indeed, it was only the finding of a small theropod tooth by Dr. Ware in November 1974 that prompted my search for mammal fossils at Kirtlington.

Finally, as Mellett pointed out, his hypothesis causes problems in certain aspects of vertebrate palaeoecology. In particular, coprocoenosis would be expected to produce a heavy preservational bias in favour of small-size animals, which are more likely to be eaten whole. Thus while the observed small size of Mesozoic mammals may well be a genuine reflection of the ecological constraints placed upon them by the dinosaurs (see, for example, Desmond 1975), it should be recognized that the actual data of the fossil record may be unreliable in this regard. Secondly, even within the size range of the animals whose preservation would be favoured by coprocoenosis, there would be subtle factors at work that would cause certain species to be selectively preserved at the expense of the others, for example, the taste preferences of the predator and the evasiveness of its prey. It is therefore a highly dangerous practice to assume that a given Mesozoic mammal fossil assemblage *even approximately* represents the live fauna from which it was derived. In this regard the qualitative and quantitative differences between the assemblages of mammal fossils from Stonesfield, the Isle of Skye, Watton Cliff, Dorset, and Kirtlington are especially noteworthy, as in these cases stratigraphic and palaeogeographic differences are minimal (see Table 4).

THE MAMMALIAN FAUNA

Except for FM/K 43, all the specimens from Kirtlington described in this section are the more important finds from the first 525.9 kg of the mammal bed to be processed, the collection being summarized in Table 3. The specimen numbers which are prefixed by 'FM/K' (Forest Marble/Kirtlington) are those used in the author's collection; the corresponding numbers of the British Museum (Natural History) are given in the Appendix. Other specimens with numbers prefixed by 'M', 'R', or 'B.M.(N.H.)' are also in the national collection.

The Scanning Electron Micrographs used to illustrate this account were taken after the specimens had been coated with aluminium, the use of which allows the specimens to be cleaned afterwards by immersion in a dilute aqueous solution of a weak alkali, such as 'Decon'.

TABLE 4. Assemblages of mammal fossils from four Middle Jurassic localities, showing the disparity in faunal elements.

CHEEK TEETH OF	Stonesfield	Isle of Skye	Watton Cliff	Kirtlington
Amphitheria	31 in 4 jaws		2 + [1]	7 + [2]
Dryolestidae			1	2
Kuehneotheriidae				2 + [1]?
Amphilestidae	42 in 7 jaws		1	
Morganucodontidae			1 + [4]	3 + [3] + [1]?
Docodontidae		9 in 2 jaws	1	2 + [5]
Triconodonta incert.sed.				[4]
Multituberculata			5	
Tritylodontidae	7 in 2 jaws	4		[4]
CANINES, INCISORS and INDETERMINATE	9 in 3 jaws		1 + [6]	4 + [9]

Sources of data: Stonesfield, Simpson 1928; Isle of Skye, Waldman and Savage 1972; Watton Cliff, author's examination of David Ward's collection from 90.5 kg of sediment (specimen numbers M 34984-M 35007 inclusive); Kirtlington, author's collection from 525.9 kg of sediment. For convenience FM/K 31, an incomplete possible eupantothere upper molar, has been omitted from the table, as has FM/K 43, an incisor of either a multituberculate or a tritylodontid. Square brackets enclose the numbers of 'incomplete' specimens as defined in the text.

Terminology relating to dental morphology is generally as explained in Patterson 1956, except where otherwise indicated. The term 'buccal' is synonymous with 'external', 'lingual' is synonymous with 'internal', while for the cheek teeth 'mesial' approximates to 'anterior' and 'distal' to 'posterior'.

The classification of Mesozoic mammals is at present an area of debate, and even controversy. In this account, unless otherwise stated, the formal taxonomy at the subclass level and lower follows the schemes outlined in Kermack, Kermack, and Mussett (1968) and in Kermack, Mussett, and Rigney (1973). This is done partly for reasons of internal consistency, and partly to facilitate comparison of the present account with the particularly relevant work of Clemens and Mills (1971). No value judgement is intended, and it may well be that the forms described herein will finally be classified in a manner other than that currently employed.

For the taxonomy at the level of the class, I favour the opinion of Bakker (1975), who groups together the Therapsida and the Mammalia (as understood to consist of the subclasses Theria and Atheria). However, unlike Bakker, I consider that the simple enlargement of the pre-existing class Mammalia achieves this purpose quite satisfactorily, and that a new class name, Bakker's Theropsida, is unnecessary. There

is an increasing body of evidence to suggest that at least certain members of the Therapsida possessed what in a living mammal would be considered highly diagnostic characteristics, namely an endothermic metabolism and an insulating layer of hair (see Ager 1977). Inclusion of the Therapsida in the Mammalia would also collect together what is essentially a unified evolutionary complex, instead of dividing it between the classes Reptilia and Mammalia, which is inevitable if an artificially rigid definition of the Mammalia is attempted by means of osteological (and especially dental) characters alone.

SYSTEMATIC DESCRIPTIONS

Class MAMMALIA Linnaeus

Subclass THERIA Parker and Haswell

Infraclass PANTOTHERIA Simpson

Order EUPANTOTHERIA Kermack and Mussett

Suborder AMPHITHERIA Kermack, Kermack, and Mussett

Family KUEHNEOTHERIIDAE Kermack, Kermack, and Mussett

Genus CYRTLATHERIUM gen. nov.

Type and only known species. *Cyrtlatherium canei* sp. nov.

Derivation of name. From Cyrtla, an Anglo-Saxon proper name and the root of Kirtlington, and therios, Greek for 'wild beast'.

Diagnosis. Lower molars with a recurved protoconid, more gracile than in *Kuehneotherium praecursoris* Kermack, Kermack, and Mussett. Lingual cingulum strongly curved upwards underneath the protoconid.

Cyrtlatherium canei sp. nov.

Plate 15, figs. 2-5

1976 FM/K 38; Freeman, pp. 1053-1054, fig. 2c.

Derivation of trivial name. To honour Derek J. Cane, who contributed so much to this exercise, and who found the holotype.

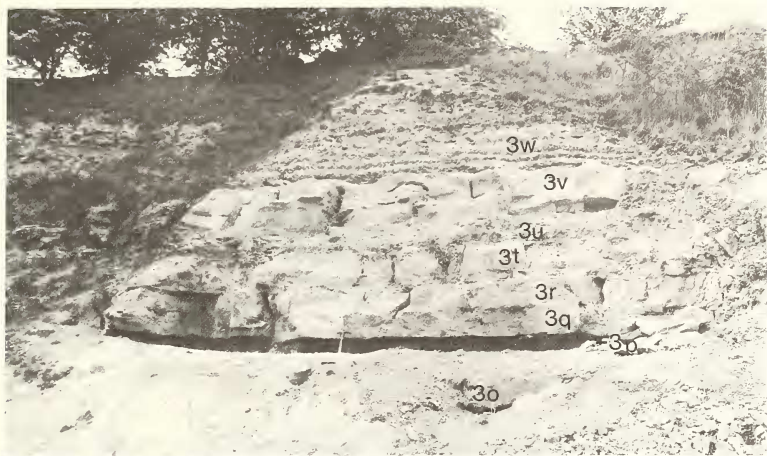
Holotype. FM/K 11, Kirtlington Mammal Bed, Upper Bathonian, Kirtlington.

Diagnosis. As for genus.

EXPLANATION OF PLATE 15

Fig. 1. Newly excavated section in the Old Cement Works Quarry, Kirtlington, showing part of the outcrop of the Kirtlington Mammal Bed (Bed 3p), June 1976. The photograph is centred on Section B (see text-fig. 1), and corresponds roughly to the upper part of plate 9 in McKerrow *et al.* 1969. The horizontal distance across the photograph is c. 7.5 m, the mammal bed extending for another c. 10 m to the left (NW.) and for another c. 4 m to the right (SE.).

Figs. 2-5. *Cyrtlatherium canei* gen. et sp. nov. 2, 3, 4, holotype (FM/K 11), lower molar from buccal ($\times 44$), occlusal ($\times 57$), and lingual ($\times 52$) aspects. 5, lower molar FM/K 38 from lingual aspect ($\times 40$). Figs. 2-4 stereophotographs.



Description. This taxon is based on two right lower molars. The holotype (FM/K 11) is complete except for the lower parts of its roots. Its protoconid is much higher than the metaconid and paraconid, and is recurved near its tip. In contrast to the specimens illustrated for *K. praecursoris* (Kermack *et al.* 1968), the paraconid is in line with the protoconid, and is not displaced lingually to any extent. A marked crest runs along the mesiolingual face of the protoconid from the tip of the protoconid to the tip of the paraconid; this does not appear to be an artefact of wear, but rather is an original feature of the tooth. In general, the tooth appears not to be worn to any significant degree. The metaconid is displaced to the lingual side of the protoconid, indeed to quite a considerable extent; as a consequence the angle of the trigonid is approximately 140°. A cingulum extends along the whole length of the lingual face, curving upwards in a manner reminiscent of the amphilestids. It extends around the ends of the tooth, to fade away at the mesial and distal ends of the buccal face. An accessory cusp occurs on the cingulum at its distal extremity (the 'hypoconulid' of Kermack *et al.* 1968), but not at its mesial extremity.

The other tooth (FM/K 38) lacks its paraconid and mesial root through breakage. As in the holotype, a prominent crest runs from the tip of the protoconid down its mesiolingual face. In general, the cingulum resembles that of the holotype, but the distal accessory cusp is a more prominent feature. The distal root is complete, tapers gently towards its apex, and curves in a mesial direction.

Finally, a badly worn and incomplete tooth (FM/K 27) is assigned with reservations to *C. canei*. It adds nothing significant to the knowledge of the taxon.

Dimensions (in mm)	FM/K 11	FM/K 38	FM/K 27
Length of crown	0.83	>0.73	>0.83
Maximum width of crown	0.37	0.37	0.34
Height of protoconid (from gum line)	0.57	0.56	>0.54

Comments. While, for reasons previously explained, I have formally classified *Cyrtolatherium* and the other kuehneotheriids within Kermack *et al.*'s Amphitheria, and not within the Symmetrodonta, I do in fact favour the latter placement. This reflects my opinion that *Kuehneotherium* is not part of a group that is ancestral to both of the orders Symmetrodonta and Pantotheria (in the sense of Patterson 1956). In the original description of *Kuehneotherium*, Kermack *et al.* (1968) attached great importance to the lingual cingulum of the upper molars, which they considered to be the precursor of the protocone; as thus interpreted, *Kuehneotherium* shows that the evolution of the protocone was underway in Rhaeto-Liassic times. However, this conclusion is not supported by the later therians *Palaeoxonodon* and *Peramus*, neither of which have even rudimentary protocones in their supposed upper molars. *Kuehneotherium* is also disqualified as the ancestor of the order Pantotheria (*sensu* Patterson) by the pronounced lingual cingula of its lower molars, the like of which are not seen in the early therians outside of the Symmetrodonta.

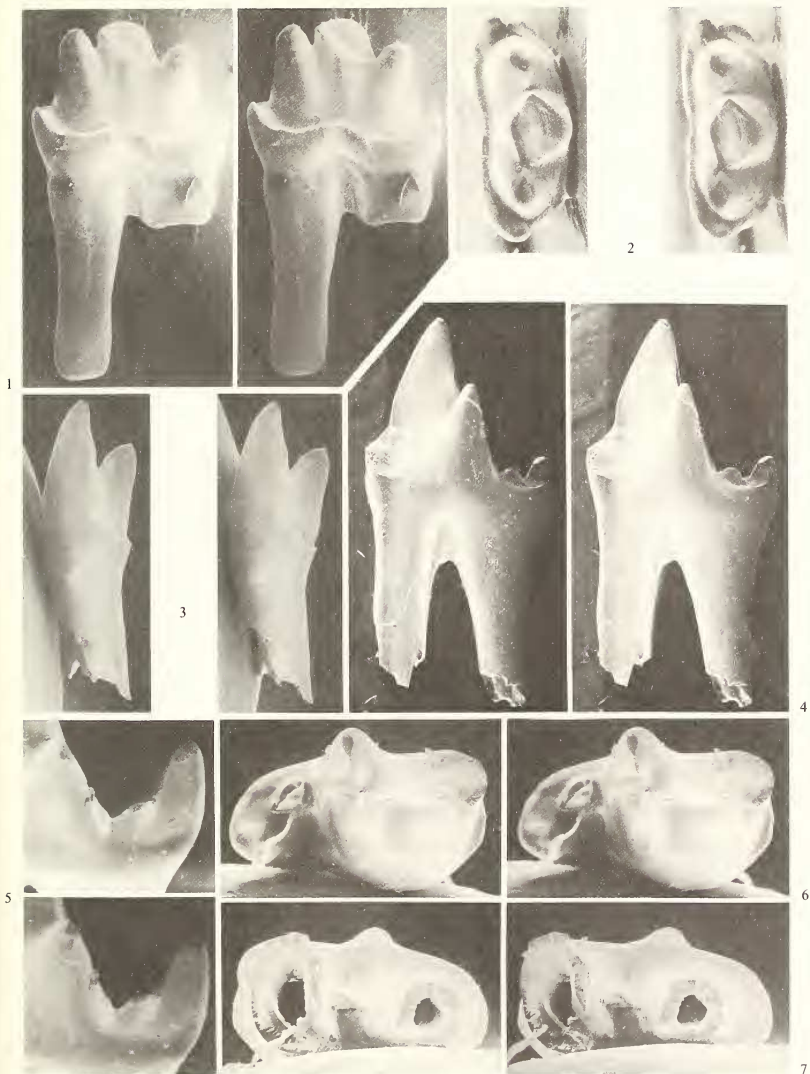
Cyrtolatherium is not the first symmetrodont to be described from the Middle Jurassic, being anticipated for over a century by the amphilestids from Stonesfield. However, the latter are not conventionally recognized as such, and are usually regarded as early triconodonts. Only recently has this assignment been questioned

EXPLANATION OF PLATE 16

Figs. 1-2. *Amphilestes broderipii* (Owen), lower molar from the Forest Marble of Watton Cliff, Dorset (M 35000), from lingual ($\times 26$) and occlusal ($\times 30$) aspects.

Figs. 3-7. *Palaeoxonodon oolithicus* Freeman. Holotype (FM/K 8), lower molar. 3, mesial aspect ($\times 37$). 4, lingual aspect ($\times 44$). 5, oblique lingual view of the talonid ($\times c. 72$). 6, occlusal aspect ($\times 56$). 7, apical aspect ($\times 56$).

Figs. 1-7 stereophotographs.



FREEMAN, Jurassic mammals

and an excellent set of arguments put forward for placing the amphilestids with the symmetrodonts (Mills 1971). Through the kindness of David Ward, I have had the opportunity to examine a lower molar of *Amphilestes broderipii* from the Forest Marble of Watton Cliff, Dorset. The specimen (M 35000) is the first material of *Amphilestes* to be seen free of matrix and as thus seen the resemblance to the lower molars of the typical symmetrodonts is compelling (see Pl. 16, figs. 1, 2). In particular, the concave lingual face and the lingual displacement of the accessory cusps (now the paraconid and metaconid) are well shown.

After revision to accommodate the above changes, the classification of the infra-class Pantotheria becomes:

Infraclass Pantotheria

Order Eupantotheria Kermack and Mussett

Suborder Amphitheria Kermack, Kermack, and Mussett

Family Amphitheriidae Owen

Family Paurodontidae Marsh

Family Peramuridae Kretzoi

Suborder Dryolestoida Butler

Family Dryolestidae Marsh

Suborder Symmetrodonta Simpson

Family Amphidontidae Simpson

Family Amphilestidae Kühne

Family Kuehneotheriidae Kermack, Kermack, and Mussett

Family Palaeotheriidae Marsh

The removal of the Amphilestidae from the subclass Atheria leaves the suborder Eutriconodonta Kermack, Mussett, and Rigney with only one family, the Triconodontidae Marsh.

Family (?) PERAMURIDAE Kretzoi
Genus PALAEOXONODON Freeman, 1976

Type and only known species. *Palaeoxonodon ooliticus* Freeman, 1976.

Derivation of name. From palaeos, Greek for 'ancient', oxonia, the Latinized name of Oxfordshire, and odons, Greek for 'tooth'.

Palaeoxonodon ooliticus Freeman, 1976

Plate 16, figs. 3-7, Plate 17, figs. 1-4, 8, Plate 18

1976 *Palaeoxonodon ooliticus* Freeman, pp. 1053-5, figs. 1a-c.

Derivation of trivial name. From the Great Oolite Series, Middle Jurassic.

EXPLANATION OF PLATE 17

Figs. 1-4. *Palaeoxonodon ooliticus* Freeman. Lower molar FM/K 7. 1, lingual aspect ($\times 49$). 2, oblique distal aspect ($\times 51$). 3, occlusal aspect ($\times 52$). 4, mesial aspect ($\times 48$).

Figs. 5-7. *Amphitherium* sp. Incomplete lower molar FM/K 16. 5, lingual aspect ($\times 25$). 6, oblique distal aspect ($\times 25$). 7, oblique mesial aspect ($\times c. 25$).

Fig. 8. *Palaeoxonodon ooliticus* Freeman. Lower premolar FM/K 9, from buccal aspect ($\times 35$).

Figs. 2-4, 7, stereophotographs.



Description. The holotype (FM/K 8) is a right lower molar, complete except for its paraconid and the lower extremities of both roots, and the buccal side of the mesial root. The protoconid is high, sharply acute, and has a recurved mesial edge. Its lingual face is roughly planar, giving the cusp an approximately semicircular cross-section. The metaconid is roughly two-thirds the height of the protoconid, and appears to have been quite sharply separated from the now-missing paraconid; no cingulum joins the bases of these two cusps. The mesial face of the protoconid bears only a poorly developed anterobuccal cingulum (see Pl. 16, fig. 3), which contrasts with the condition seen in *Amphitherium* and *Peramus*, and in the dryolestid teeth described later in this account.

Most of the interest of the holotype lies in its talonid, which appears to be roughly intermediate in form between those seen in *Amphitherium prevostii* (Middle Jurassic) and *Peramus tenuirostris* (Late Jurassic), and foreshadows those of tribosphenic dentitions. As in *Amphitherium*, the talonid of FM/K 8 consists primarily of a single cusp (the hypoconid?) situated on the distobuccal end of a crista obliqua that extends from the distal edge of the metaconid and which forms a continuation of the crest on the metaconid. However, unlike *Amphitherium*, the crista obliqua is raised into a small cusp at its approximate median point, in which feature it resembles certain specimens of *Peramus*, 'Trinity molar type 6' (Slaughter 1971), and certain Tertiary Insectivores (see *Scraeva* and *Arvaldus* in Cray 1973). Following Mills (1964), this median cusp is called the 'posterior accessory cusp' in this account. From the ?hypoconid a low ridge runs in an arc mesiolingually towards the base of the metaconid. This low ridge and the crista obliqua together encompass an area which is concave and includes the lingual face of the ?hypoconid; this would seem to be an initial stage in the development of the talonid basin which was to become so important in the later stages of mammalian dental evolution. It is possible that the concavity of the ?hypoconid in *Palaeoxonodon* assisted a piercing function of the cusp, after the fashion of a fuller on a bayonet or stabbing knife. The low ridge that forms the lingual rim of the incipient talonid basin of FM/K 8 is expanded in two places to form what from their positions appear to be incipient developments of an entoconid and a hypoconulid. Although these incipient cusps are barely perceptible, they are sufficiently elevated above the ridge from which they arise to have been preferentially abraded (see Pl. 16, fig. 6). Their positions seem to indicate that the first of the talonid cusps to evolve, i.e. the one seen in *Amphitherium*, was the hypoconid (for a summary of the arguments on this topic, see Slaughter 1971, pp. 138-140).

Another right lower molar (FM/K 7) is similar to the holotype but has lower trigonid and talonid cusps. In the case of FM/K 7 there is no anterobuccal cingulum at all, and the talonid comprises only one cusp (the ?hypoconid), the other two talonid cusps not being seen even under the Scanning Electron Microscope (see Pl. 17, figs. 2 and 3). Also, there is no development at all of a talonid basin, the lingual face of the ?hypoconid being entirely convex. As in the holotype, there is a 'posterior accessory cusp' upon the crista obliqua.

A premolar (FM/K 9) has a single recurved cusp with a buccal cingulum that ends distally in a small heel. It has two roots which are separated only near their lower extremities (see Pl. 17, fig. 8). The specimen is doubtfully identified as a left lower premolar of *P. ooliticus*, primarily because of its size and its general resemblance to the lower premolars of *Amphitherium* and *Peramus*.

In the light of the remarks made earlier regarding the origins of the mammal fossils, it may be significant that FM/K 7, FM/K 9, and the holotype all came from the same 39.5 kg batch of sediment.

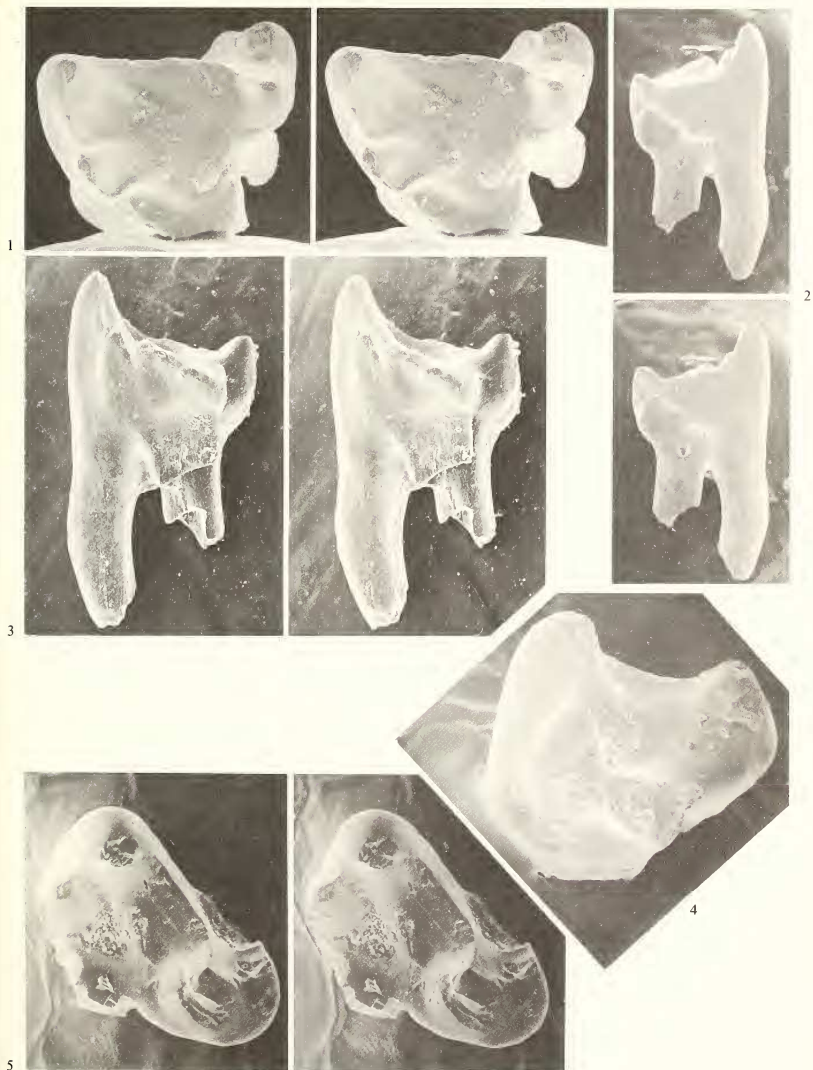
Dimensions (in mm)

	FM/K 8	FM/K 7	FM/K 9
Length of crown	>0.87	>0.90	0.51
Length of trigonid	>0.59	>0.63	—
Maximum width of crown	0.49	0.54	
Height of protoconid (from gum line)	0.89	0.80	0.61

EXPLANATION OF PLATE 18

Figs. 1-5. *Palaeoxonodon ooliticus* Freeman. Referred upper molar FM/K 12. 1, occlusal aspect ($\times$ c. 52). 2, mesial aspect ($\times$ 28). 3, distal aspect ($\times$ 38). Referred hindmost upper molar FM/K 4. 4, oblique distal aspect ($\times$ 50). 5, occlusal aspect ($\times$ 50).

Figs. 1-3, 5, stereophotographs.



FREEMAN, Jurassic mammals

Three eupantothere upper molars are also referred to *Palaeoxonodon ooliticus*, largely on account of their size, and at the risk of engaging in a circular argument, because they are generally similar to those presumed, on better evidence, to be of *Peramus tenuirostris* (see Clemens and Mills 1971).

Specimen FM/K 12 is a superbly preserved left upper molar, complete except for its two buccal roots. The paracone is the highest cusp of the crown, and forms its most lingual feature. Consider firstly the distal edge of the tooth, apart from the paracone it bears in all four cusps. The metacone is immediately distolingual to the paracone, from which it is only incompletely separated. From the gum-line the heights of the paracone and metacone are in the approximate ratio 2:1. A metacrista runs distobuccally from the metacone, and bears three small, incompletely separated cusps, of which the one adjacent to the metacone is the largest; in position it corresponds with the virtually obsolete cusp labelled 'cusp c' in the figure of the *Peramus* upper molar in Crompton (1971). As to the mesial edge of the tooth, the paracrista runs mesio-buccally from the paracone to end at the buccal edge of the tooth in a prominent stylocone. In FM/K 12 the stylocone is distinctly mesial to the position of the stylocone in the dryolestids, where it forms a prominent feature near the middle of the buccal edge of the tooth (the centroexternal cusp of Simpson 1929). As in the case of the 'cusp c', the stylocone of FM/K 12 is more developed than in *Peramus*, and is comparable to the corresponding feature in *Pappotherium pattersoni* (Middle Cretaceous) (see Slaughter 1971). However, unlike *Pappotherium*, there is no protocone on the lingual side of the paracone; indeed, there is not even a lingual cingulum that could be considered to be a forerunner of the protocone.

FM/K 30 is a much less complete left upper molar, as it lacks the buccal side of the tooth, i.e. the stylocone, parastyle, and the end of the metacrista. What remains of the distal edge of the tooth bears two cusps apart from the paracone: as in FM/K 12 the metacone is distobuccally situated with respect to the paracone, but is more distinctly separated from it. The 'cusp c' is also a more sharply defined feature than in FM/K 12, and in general what remains of the tooth resembles the unidentified specimen FM/K 32 (see Pl. 19, figs. 1-3).

The third of the upper molars referred to *Palaeoxonodon ooliticus* (FM/K 4) differs from the other two in its distal edge, which is markedly shorter than the mesial and bears only two cusps, the paracone and the metacone. In spite of the damage (apparently *post mortem*) that it has suffered, the short metacrista does not appear to have borne a 'cusp c' or other cusps. As in FM/K 12, the paracone and metacone are only partially separated from one another. The form of the tooth suggests that it is a hindmost left upper molar.

Dimensions (in mm)

	FM/K 12	FM/K 30	FM/K 4
Length of crown	0.95	>0.75	>0.84
Width of crown	0.96	>0.85	0.99
Height of paracone (from gum line)	0.80	0.82	c. 0.6

Family ?AMPHITHERIIDAE Owen

?*Amphitherium* sp.

Plate 17, figs. 5-7

Description. A eupantothere left lower molar (FM/K 16), minus its talonid, is distinguished from *P. ooliticus* by its larger size, the slightly convex lingual face of the protoconid, and by its prominent anterobuccal cusp. From the size of the scar left by the removal of the talonid, it must have been a sizeable structure, the tooth thus differing from the teeth of the dryolestids described later. In general what remains of the tooth resembles the molars of *A. prevostii*, but in the absence of the talonid a positive identification, even at the level of the family, is not possible.

EXPLANATION OF PLATE 19

Figs. 1-6. Eupantothere upper molars. Unworn specimen FM/K 32. 1, oblique occlusal aspect ($\times 34$). 2, oblique mesial aspect ($\times c. 38$). 3, distal aspect ($\times 37$). Worn specimen FM/K 26. 4, mesiobuccal aspect ($\times 47$). 5, distal aspect ($\times 47$). 6, oblique occlusal aspect ($\times 38$).

Figs. 1, 3, 6, stereophotographs.



1



2



3



4



5



6



Dimensions:

Length of trigonid 0.79 mm.
 Maximum width of trigonid 0.75 mm.
 Height of protoconid (from gum line) 1.02 mm.

Compare with *A. prevostii* B.M.(N.H.) 36822, from the Stonesfield Slate (dimensions in mm).

	M ₅	M ₄	M ₃	M ₂	M ₁	P ₄
Length of crown	1.10	1.69	1.06	1.11	1.04	0.85
Length of trigonid	0.81	0.89	0.86	0.81	0.73	—
Maximum width of trigonid	0.73	0.69	0.65	0.61	0.65	—
Height of protoconid (from gum line)	1.02	1.08	1.08	1.08	0.98	—

Suborder AMPHITHERIA Kermack, Kermack, and Mussett
 Family INCERTAE SEDIS

Plate 19, figs. 1-6

1976 FM/K 32; Freeman, p. 1054, figs. 2a, b.

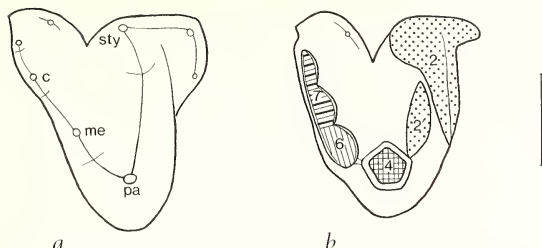
Description. Two right upper molars have been found which are significantly larger than the three assigned to *P. ooliticus*, although they are otherwise generally similar to them. They are roughly compatible in size with the lower molar described above as *?Amphitherium* sp., although any such identification in this case must be little more than a guess.

Specimen FM/K 32 is a complete, virtually unworn, crown supported on the remnants of three roots. As in the upper molars referred to *P. ooliticus*, the stylocone is a prominent cusp, situated on the buccal edge of the tooth in a position distinctly mesial to the line that bisects the tooth through the paracone. Once again the paracone is the largest of the cusps, and forms the most lingual part of the tooth. The metacone is quite distinct from the paracone, and is situated distobuccally with respect to it, more so than in the case of FM/K 12. In addition, the metacrista that runs distobuccally from the apex of the metacone bears only two cusps, both of which are quite separate from one another, (see Pl. 19, figs. 1-3 and text-fig. 2a).

In contrast, specimen FM/K 26 has been subjected to extensive wear, apparently before death (see Pl. 19, figs. 4-6, and text-fig. 2b). This has resulted in the truncation of the paracone (Facet 4), and the removal of the metacone and the other cusps on the distal edge of the crown to leave an elongated concavity in their stead (Facet 6+7). On the mesial side of the crown the stylocone has largely been removed by an extensive wear facet (2) that runs obliquely to the mesiobuccal extremity of the parastyle, little of which now remains. The mesial crest of the paracone has also been worn away to leave an elongated concavity (Facet 2'). The ornament and numbering of the wear facets in text-fig. 2b follows that used in the figure of the *Eurylambda* upper molar in Crompton and Jenkins 1967, where the pattern of wear is markedly similar. Crompton and Jenkins assign their facets 2 to wear against the apex of a metaconid of an opposing lower molar, while facets 4, 6, and 7 were produced by occlusion against, respectively, the mesial cingulum cusp, the paraconid, and the protoconid of the lower molar situated behind that responsible for facets 2. However, facets 3 and 5 on the mesiolingual and distolingual faces of the paracone of *Eurylambda* are not represented at all in FM/K 26; from Crompton and Jenkins's figure these two facets were produced by, respectively, the distobuccal and mesiobuccal surfaces of the two adjacent lower molars that abutted the upper molar.

Nor is FM/K 26 alone in failing to display wear facets on the lingual side of the paracone. The minimal amount of wear on FM/K 32 is fully in accord with that seen on FM/K 26, and if extrapolated would produce a tooth of identical appearance. As other workers have reported or predicted wear facets on the lingual side of the paracone, and in particular between the metacone and paracone (see, for example, Mills 1964, Clemens and Mills 1971, p. 105, and Crompton 1971), their manifest absence in FM/K 26 should be noted.

Dimensions (in mm)	FM/K 32	FM/K 26
Length of crown	1.11	1.02
Width of crown	1.20	1.10
Height of paracone (from gum line)	1.06	>0.83



TEXT-FIG. 2. Eupantotheres upper molars from occlusal aspect; unworn (fig. 2a, FM/K 32) and worn (fig. 2b, FM/K 26). Abbreviations: pa., paracone; me., metacone; c, cusp 'c'; sty., stylocone. The scale bar represents 0.5 mm.

Suborder DRYOLESTOIDEA Butler
Family DRYOLESTIDAE Marsh

Plate 20, figs. 1-8

1976 FM/K 29; Freeman, p. 1053, fig. 2d-f.

Description. This family is represented in the collection from Kirtlington by two incomplete lower molars.

Specimen FM/K 29 is a left lower molar which lacks its talonid and the greater part of its roots. As is typical of the dryolestids, its trigonid is mesiodistally compressed compared to *Palaeoxonodon*, the ratio H/L' of the height of the protoconid (H) to the length of the trigonid (L') being 1.70-2.38 for FM/K 29 (the uncertainty is caused by doubts as to the exact position of the base of the protoconid), but less than 1.51 and 1.27 for the two lower molars of *Palaeoxonodon*. Although the talonid has been removed by breakage, the scar that it has left indicates that it must have been a small structure situated low on the distal flank of the metaconid. Again in contrast to *Palaeoxonodon*, the crista obliqua does not extend to the tip of the metaconid. A prominent and distinctly pointed cuspule occurs on the mesial face of the protoconid. The paraconid and metaconid are of comparable size, and are distinctly smaller than the protoconid. The roots appear to have been much closer together than in *Palaeoxonodon*, the mesial root having an elliptical cross-section, not circular as in the holotype of *P. ooliticus*.

Specimen FM/K 14, a right lower molar, is even less complete than FM/K 29, as it lacks its talonid and roots, and much of its metaconid. In general it is similar to FM/K 29 in the proportions and dispositions of its cusps, but differs in the joining of the bases of the paraconid and metaconid by a distinct cingulum. As before, the ratio H/L' is greater (1.93) than in the material of *Palaeoxonodon*.

Dimensions (in mm)

	FM/K 29	FM/K 14
Length of trigonid	0.56	0.61
Maximum width of trigonid	0.58	0.55
Height of protoconid (from gum line)	0.95-1.33	1.18

Order (?) EUPANTOTHERIA Kermack and Mussett

Specimen FM/K 31 is incomplete, consisting of two well-separated and acute cusps, supported on a single stout root. The fossil may be a eupantotheres left upper molar of a type unlike those previously described, i.e. with a metacone lying directly distal to the paracone, instead of mesiodistally to it. Once again, there is no lingual cingulum.

Dimensions:

Height of ?paracone from gum line 0.67 mm.

Height of ?metacone from gum line 0.58 mm.

Subclass ATHERIA Kermack, Mussett, and Rigney
 Order TRICONODONTA Osborn
 Suborder MORGANUCODONTA Kermack, Mussett, and Rigney
 Family MORGANUCODONTIDAE Kühne
 Genus WAREOLESTES gen. nov.

Type and only known species. Wareolestes rex sp. nov.

Derivation of name. After Dr. Martin Ware, in recognition of his major contribution to the success of my work at Kirtlington; and *lestes*, Greek for 'brigand', alluding to the presumed carnivorous nature of the animal.

Diagnosis. Lower molars with kühnecone directly lingual to the main cusp, and much smaller than the main cusp. Lower molars with a poorly defined buccal cingulum.

Wareolestes rex sp. nov.

Plate 21, figs. 1, 2

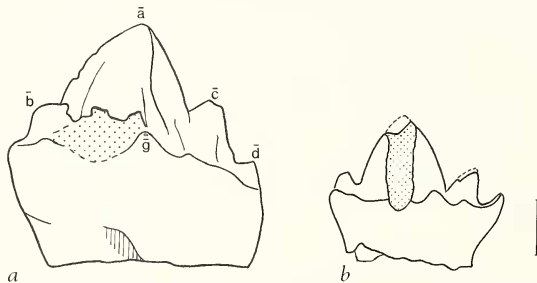
1976 FM/K 25; Freeman, pp. 1053-4, fig. 2g.

Derivation of trivial name. From the Latin for 'king', an allusion to the relatively large size of the animal and also a pun on the name of Mr. E. J. King.

Holotype. FM/K 25, Kirtlington Mammal Bed, Upper Bathonian, Kirtlington.

Diagnosis. As for genus. Upper Bathonian.

Description. The holotype and only known specimen is a well-preserved nearly complete lower molar. It is substantially larger and more inflated in shape than the lower molars of the triconodont from the Welsh Rhaeto-Liassic fissures (Kühne 1949; Parrington 1967). However, in most other respects, especially in the distribution and relative proportions of its principal cusps, the holotype of the new species is similar to the Welsh form (see text-fig. 3). In particular, both have a high central cusp ($\bar{a}$, using the nomenclature of



TEXT-FIG. 3. Morganucodontid lower molars from lingual aspect. Fig. 3a, holotype of *Wareolestes rex*, FM/K 25. Fig. 3b, Welsh Rhaeto-Lias triconodont, M 16536. The scale bar represents 0.5 mm.

EXPLANATION OF PLATE 20

Figs. 1-8. Dryolestid lower molars. Specimen FM/K 29. 1, lingual aspect ($\times 50$). 2, distal aspect ($\times 45$). 3, mesial aspect ($\times 45$). 4, apical aspect ($\times c. 75$). 5, occlusal aspect ($\times c. 75$). Specimen FM/K 14. 6, lingual aspect ($\times 48$). 7, distal aspect ($\times 45$). 8, mesial aspect ($\times 45$).
 Figs. 1-3, 6, stereophotographs.



2



4



5



6



7



8

Crompton and Jenkins 1968), in line mesially and distally with two smaller cusps ($\bar{b}$ and $\bar{c}$ respectively), and an expanded lingual cingulum on which are developed a series of small cusps. In FM/K 25 there are three of these cingulum cusps preserved; they have the same relative sizes as in the Welsh triconodont, with the present central cusp being the highest. Wear or damage may have removed additional cusps originally present on the lingual cingulum mesiolingual to the main cusp. In contrast to the Welsh triconodont, the highest cingulum cusp (the kühnecone or cusp $\bar{g}$) of FM/K 25 is displaced mesially to a position directly lingual to the main cusp ($\bar{a}$), instead of being lingual to the valley between cusp $\bar{a}$ and the distal cusp $\bar{c}$. The lingual cingulum curves around the distal edge of the tooth where a substantial cusp ($\bar{d}$) arises from it, directly distal to the distal cusp $\bar{c}$. The cingulum then continues in a subdud, non-cuspidate, form around the buccal face of the crown, in which feature it contrasts with the lower molars of the Welsh triconodont.

The lingual face of the main cusp ($\bar{a}$) is divided into four shallow embayments, giving the lingual face a scalloped outline from above. The most distal of these embayments is more concave than the others, and results in the distal edge of cusp $\bar{a}$ having a sharp concavo-convex cross-section.

The crown is supported by the remains of two stout roots, both sharply broken across at their point of separation.

Dimensions: Length of tooth 2.31 mm.
Width of crown 1.24 mm.
Height of principal cusp from lingual cingulum c. 1.2 mm.

Comments. The occurrence of a typical morganucodontid in the Upper Bathonian is a substantial and unexpected upwards extension of the known stratigraphic range of the family, which hitherto has only been known from the Rhaeto-Lias. It indicates that the morganucodontids were a stable and distinctive group for at least thirty million years.

Wareolestes shows no features intermediate between the Welsh triconodont and the triconodontids of the Late Jurassic. In particular, FM/K 25 shows no sign of the equalization of the principal cusps and the elimination of the cingulum cusps seen in the lower molars of the triconodontids.

Suborder DOCODONTA Kretzoi
Family DOCODONTIDAE Simpson
?Boreolestes sp.

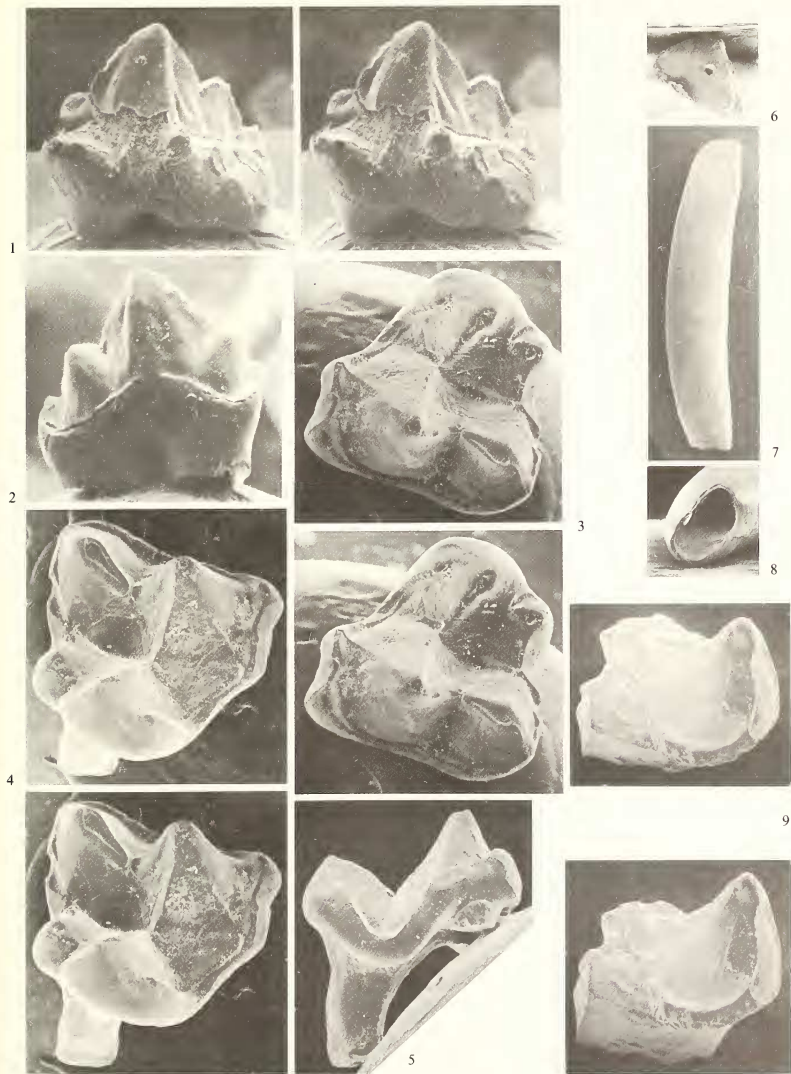
Plate 21, figs. 3-5

1976 FM/K 24; Freeman, p. 1054, fig. 2h.

Description. Only one of the docodont teeth from Kirtlington is sufficiently complete to merit description in this account. It is with great diffidence ascribed to *Boreolestes*, which is the only known Middle Jurassic docodont (Waldman and Savage 1972). Its size is of the same order as the lower molars of *Boreolestes serendipitus*.

EXPLANATION OF PLATE 21

- Figs. 1, 2. *Wareolestes rex* gen. et sp. nov. Holotype (FM/K 25), lower molar. 1, lingual aspect ($\times 19$). 2, buccal aspect ($\times 19$).
Figs. 3-5. Docodontid upper molar, FM/K 24. 3, occlusal aspect ($\times 29$). 4, linguo-occlusal aspect ($\times 28$). 5, mesial aspect ($\times 26$).
Figs. 6-8. Multituberculate or tritylodontid incisor, FM/K 43. 6, occlusal aspect ($\times 21$). 7, buccal aspect ($\times 11$). 8, apical aspect ($\times 21$).
Fig. 9. Cusp of a tritylodontid cheek tooth, FM/K 3; oblique lateral aspect ($\times 12$).
Figs. 1, 3, 4, 9, stereophotographs.



FREEMAN, Jurassic mammals

Class MAMMALIA Linnaeus (sensu lato)
 Order THERAPSIDA Broom
 Family TRITYLODONTIDAE Cope

Plate 21, fig. 9

Description. Four cusps or parts of cusps which appear to be from tritylodontid cheek teeth have been found at Kirtlington. They add nothing to the knowledge of the family, except to slightly extend its known range upwards from the Middle Bathonian to the Late Bathonian. A complete incisor (FM/K 6) is tentatively referred to the Tritylodontidae, because of its strong similarity to the *Oligokyphus* incisor R7304 (see text-fig. 4 and compare with Kühne 1956, text-fig. 38f).

Dimensions of FM/K 6:

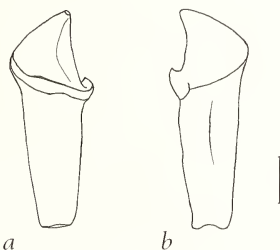
Total height of tooth 2.36 mm.

Height of crown from gum line 0.89 mm.

Length of crown 1.07 mm.

Width of crown 0.52 mm.

TEXT-FIG. 4. Possible tritylodontid incisor FM/K 6, from *a*, lingual aspect; and *b*, buccal aspect. The scale bar represents 0.5 mm.



CONCLUSIONS

With the benefit of hindsight, the mammalian fauna of the Middle Jurassic is now seen to be much as would be expected from its intermediate stratigraphic position between the Rhaeto-Liassic and the Late Jurassic faunas. Thus, on the one hand, there are the relict representatives of the Rhaeto-Lias families Morganucodontidae, Kuehneotheriidae, and Tritylodontidae, and, on the other, early members of the Late Jurassic families Dryolestidae, Docodontidae, and, possibly, Peramuridae. If the Amphilestidae are placed in the Symmetrodonta, and if the specimen described from Watton Cliff, Dorset, really is a Multituberculate (Freeman 1976*a*), then all of the major groupings of Mesozoic mammals now appear to have existed in the Middle Jurassic, with the apparent exceptions of the Eutriconodonta and the higher Theria. Even these may be awaiting discovery in some as yet unknown Middle Jurassic locality. The marked faunal differences between the known Middle Jurassic mammal sites do not inspire confidence that even now we have a fair and balanced view of the mammalian life of the Middle Jurassic.

The newly revealed diversity of the Bathonian mammalia at the level of the family, and the absence of intermediate forms suggest that the higher mammalian taxa became differentiated from one another long before the Bathonian. If the apparent faunal poverty of the Rhaeto-Lias is genuine, it would seem that the Early Jurassic

was a time of rapid mammalian diversification. On the other hand, perhaps the Rhaeto-Lias assemblages known at present are as biased and unrepresentative as the Stonesfield fauna is now shown to be. Only time will tell.

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APPENDIX

The specimens described in this paper have been deposited in the Department of Palaeontology of the British Museum (Natural History). The list below correlates the author's collection numbers (prefaced with 'FM/K') with the corresponding B.M.(N.H.) numbers (prefaced with 'M').

FM/K 1=M 36501	FM/K 18=M 36518	FM/K 35=M 36535
FM/K 2=M 36502	FM/K 19=M 36519	FM/K 36=M 36536
FM/K 3=M 36503	FM/K 20=M 36520	FM/K 37=M 36537
FM/K 4=M 36504	FM/K 21=M 36521	FM/K 38=M 36538
FM/K 5=M 36505	FM/K 22=M 36522	FM/K 39=M 36539
FM/K 6=M 36506	FM/K 23=M 36523	FM/K 40=M 36540
FM/K 7=M 36507	FM/K 24=M 36524	FM/K 41=M 36541
FM/K 8=M 36508	FM/K 25=M 36525	FM/K 42=M 36542
FM/K 9=M 36509	FM/K 26=M 36526	FM/K 43=M 36543
FM/K 10=M 36510	FM/K 27=M 36527	FM/K 52=M 36552
FM/K 11=M 36511	FM/K 28=M 36528	FM/K 53=M 36553
FM/K 12=M 36512	FM/K 29=M 36529	FM/K 54=M 36554
FM/K 13=M 36513	FM/K 30=M 36530	FM/K 58=M 36558
FM/K 14=M 36514	FM/K 31=M 36531	FM/K 60=M 36560
FM/K 15=M 36515	FM/K 32=M 36532	FM/K 61=M 36561
FM/K 16=M 36516	FM/K 33=M 36533	FM/K 62=M 36562
FM/K 17=M 36517	FM/K 34=M 36534	FM/K 63=M 36563

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